

# CHTHAMALID BARNACLES OF EASTER ISLAND; PERIPHERAL PACIFIC ISOLATION OF NOTOCHTHAMALINAE NEW SUBFAMILY AND HEMBELI-GROUP OF EURAPHIINAE (CIRRIPEDIA: CHTHAMALOIDEA)

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## ABSTRACT

*Euraphia devaneyi* new species (of the *hembeli*-group) is described from Easter Island. *Rehderella belyaevi* (Zevina and Kurshakova) new genus is given a supplementary description and its range extended from Easter Island to Pitcairn Island. Consideration of the pleisomorphies and apomorphies of *R. belyaevi* and related genera necessitates recognition of the Notochthamalinae, a new subfamily of South Pacific species with card setae on some or all of the anterior cirri. Diagnoses are given for *Notochthamalus* new genus, for *N. scabrosus* from South America, *Nesochthamalus* new genus, for *N. intertextus* from widespread west Pacific localities, and *Chamaesipho* Darwin containing three species from New Zealand and Australia. Both chthamalids of Easter Island are peripheral Polynesian endemics, and the historical biogeography of this in connection with such young islands is discussed.

Chthamalid barnacles are characteristic of rocky shores all round the world. Twenty-five species have been assigned to the genus *Chthamalus* or the closely related genus *Euraphia* (Newman and Ross, 1976; Dando and Southward, 1980). The distinction between *Chthamalus* and *Euraphia* has rested primarily on the nature of the mandible; quadridentoid with a combed lower margin in the former and tridentoid with a pectinate lower angle in the latter. Difficulties with this were raised by Pope (1965), particularly with *Euraphia intertextus* (Darwin) in which characters other than the mandible relate it to *Chamaesipho columna* (Spengler) which has a quadridentoid mandible.

Our attention was refocused on this and related matters when we examined barnacles from Easter Island. The commonest barnacle on the basalt shores there is a chthamalid described and named *Chthamalus belyaevi* by Zevina and Kurshakova (1973). It has a *Chthamalus*-like mandible yet is tridentoid, and shows clear shell relationships with *E. intertextus* of the tropical western Pacific as well as with *Chthamalus scabrosus* Darwin and *Chamaesipho* spp. of southeast and southwest shores of the South Pacific respectively. It is our conclusion that the *Chthamalus-Euraphia* dichotomy for the bulk of the six-plated chthamalid barnacles is not now adequate.

The barnacle fauna of Easter Island is meager. Only three shore species are known: a new species of *Euraphia* described herein, the chthamalid *C. belyaevi* here given a supplementary description and generically redefined, and a *Tesseropora* of small size and similar to specimens that have been collected from Norfolk Island and the Hawaiian Islands, and also reminiscent of *T. atlantica* from Bermuda and the Azores in the Atlantic Ocean (Newman and Ross, 1977). Two stalked barnacles are known: *Lepas anserifera* Linnaeus was collected on floating debris (BAF, pers. obs.) and *Temnaspis* cf. *hawaiiensis* (Pilsbry) was shown as commensal on the mouthparts of the lobster *Panulirus pascuensis* Reed by Holthuis (1972).

This paper pays particular attention to the two Easter Island chthamalids, considers their relationship to other chthamalids of the South Pacific Ocean, and

discusses the consequences to our understanding of the Chthamalidae. Questions of historical biogeography of how these species came to occur in the relatively young Easter Island have been discussed in general terms by Newman and Foster (1983), and wider implications are considered by Newman and Foster (1987).

#### SYSTEMATIC PART

##### Family CHTHAMALIDAE Darwin, 1854

##### Subfamily Euraphiinae Newman and Ross, 1976

##### (Group of *Euraphia hembeli* Conrad, Nilsson-Cantell, 1921)

*Diagnosis.*—Chthamalid barnacles with six parietal shell plates including rostrum, carina and paired latera and rostrilatera. Scutum higher than wide, interlocked but not concrescent with tergum. Mandible incisiform, tridentoid, and with pectinate lower angle. Cirri without card setae.

##### *Euraphia devaneyi* new species

Figures 1A–E, 2

*Material Examined.*—Easter Island—Two specimens, Hanga Roa, intertidal, 5 February 1965 (I. Efford coll.); several specimens, Hanga Nui, in tide pools, 30 October 1974 (H. Rehder coll., no. E-27, USNM file no. 313647, included 2nd paratype); several specimens, Moto Nui, intertidal rocks, 1 November 1974, (H. Rehder coll., no. E-33, included holotype and 1st paratype); Hanga Roa, Vinapu, Vaihu, Anakena, 20–23 November 1976 (BAF coll., included 3rd paratype lot); four specimens, from 5 m of depth on dead *Pocillopora*, Motu Nui Bay, 18 February 1983 (L. H. DiSalvo coll.).

*Deposition of Types.*—(1) Holotype, U.S.N.M. Cat. No. 233266 (dissected); (2) 1st paratype, U.S.N.M. Cat. No. 233267 (in alcohol, undissected); (3) 2nd paratype, Brit. Mus. (Nat. Hist.) Reg. No. 1987-1 (dissected); (4) 3rd paratype lot, Brit. Mus. (Nat. Hist.) Reg. No. 1987-2 (undissected).

*Distribution.*—Easter Island (Fig. 4).

*Etymology.*—Named in honor of the late Dr. Dennis Devaney, Bishop Museum, Honolulu, who provided us with the specimen of *E. hembeli* he and Dr. J. Randall collected from Pitcairn Island.

*Description.*—In uneroded specimens (Fig. 1A), shell conic, apexes of parietes projecting, externally white and strongly ribbed but deeper shell matrix grey-pink. Radii narrow with sinuous margins interlocking with adjacent parietal margin. Alae of carina wide, extending to lateral angle of orifice, midway on latera. Basal edge of parietes radially ridged. Eroded specimens externally showing pink laminae and obliterated radial sutures; internally with secondary calcification lining the entire body chamber of the shell.

Base calcareous, white; in larger specimens overlain internally and peripherally with pink ledge of secondary parietal calcification.

Scuta and terga (Fig. 1B–E) strongly interlocked but not calcified together, darkly vinaceous internally, brown externally when uneroded. Scutum very narrow, with thick articular margin elevating sinuous inner tergal margin and forming apical edge between inner and outer faces of plate; adductor muscle pit prominent; lateral depressor muscle crests at rostral and tergal angles. Tergum with strong and pectinate depressor muscle crests, spur truncated at basi-scutal angle.

*Maximum Shell Size.*—Forty-five millimeter rostrocarinal diameter, 24-mm high.

Labrum (Fig. 2A) shallowly concave, with row of minute teeth and fine setae on edge. Mandible (Fig. 2B) tridentoid, denticulate between, with closely pectinate lower angle. Maxillule (Fig. 2C) with two large spines at slightly protuberant upper

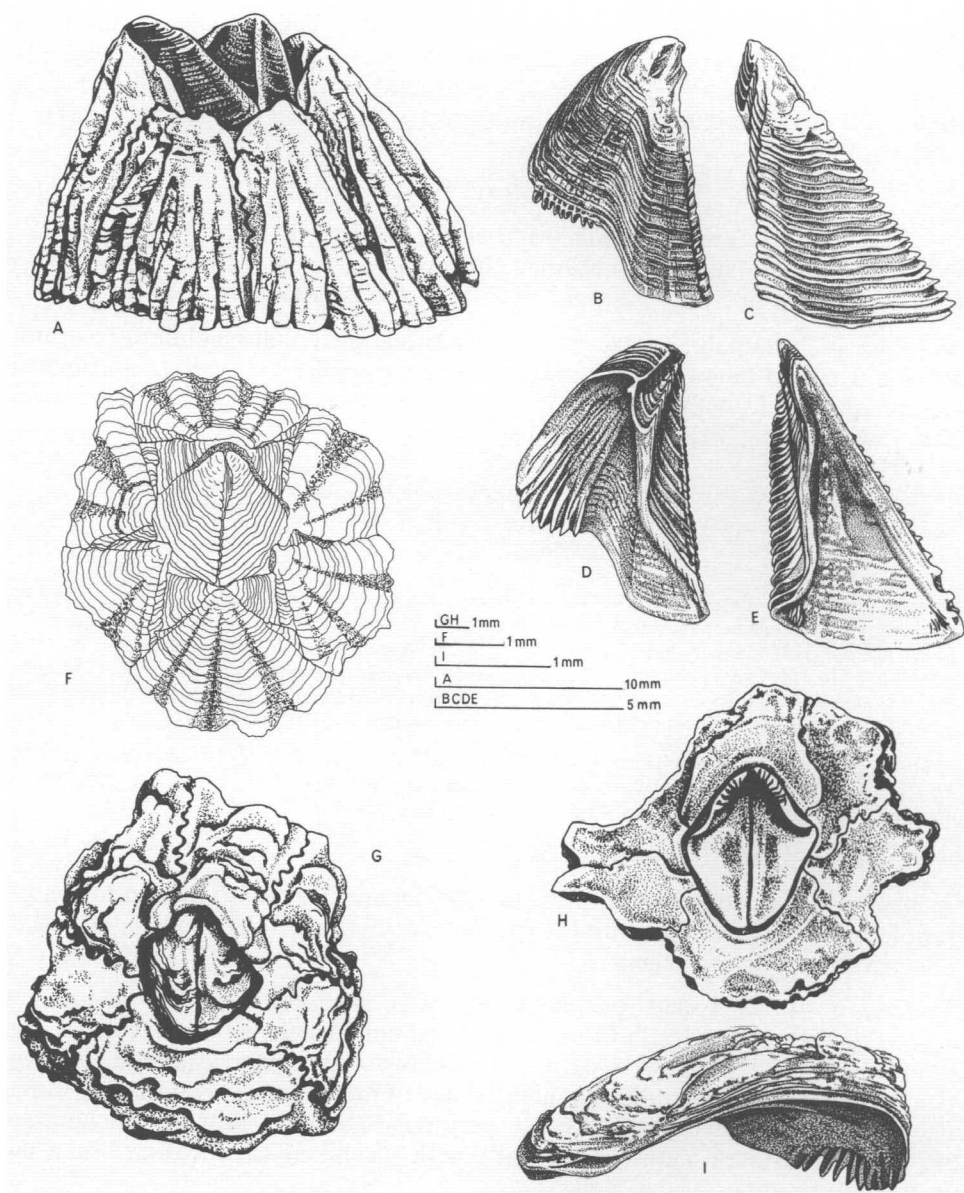


Figure 1. A-E, *Euraphia devaneyi* new sp. A, shell from left side; B-E, targa (B, D) and scuta (C, E), exterior and interior views; F-I, *Rehderella belyaevi* new genus F, juvenile from Pitcairn Island; G, H, shell from Easter Island viewed from above and below; I, fused opercula viewed obliquely from above.

angle, double row of slender spines in central part of blade, and more or less prominent lower angle with short spines. Numbers of segments in rami of cirri of two specimens as follows (anterior ramus first):

rostrocarinal diameter	I	II	III	IV	V	VI
15 mm	8, 7	6, 10	15, 16	19, 19	21, 20	20, 21
42 mm	8, 7	10, 16	17, 19	24, 27	27, 28	27, 25

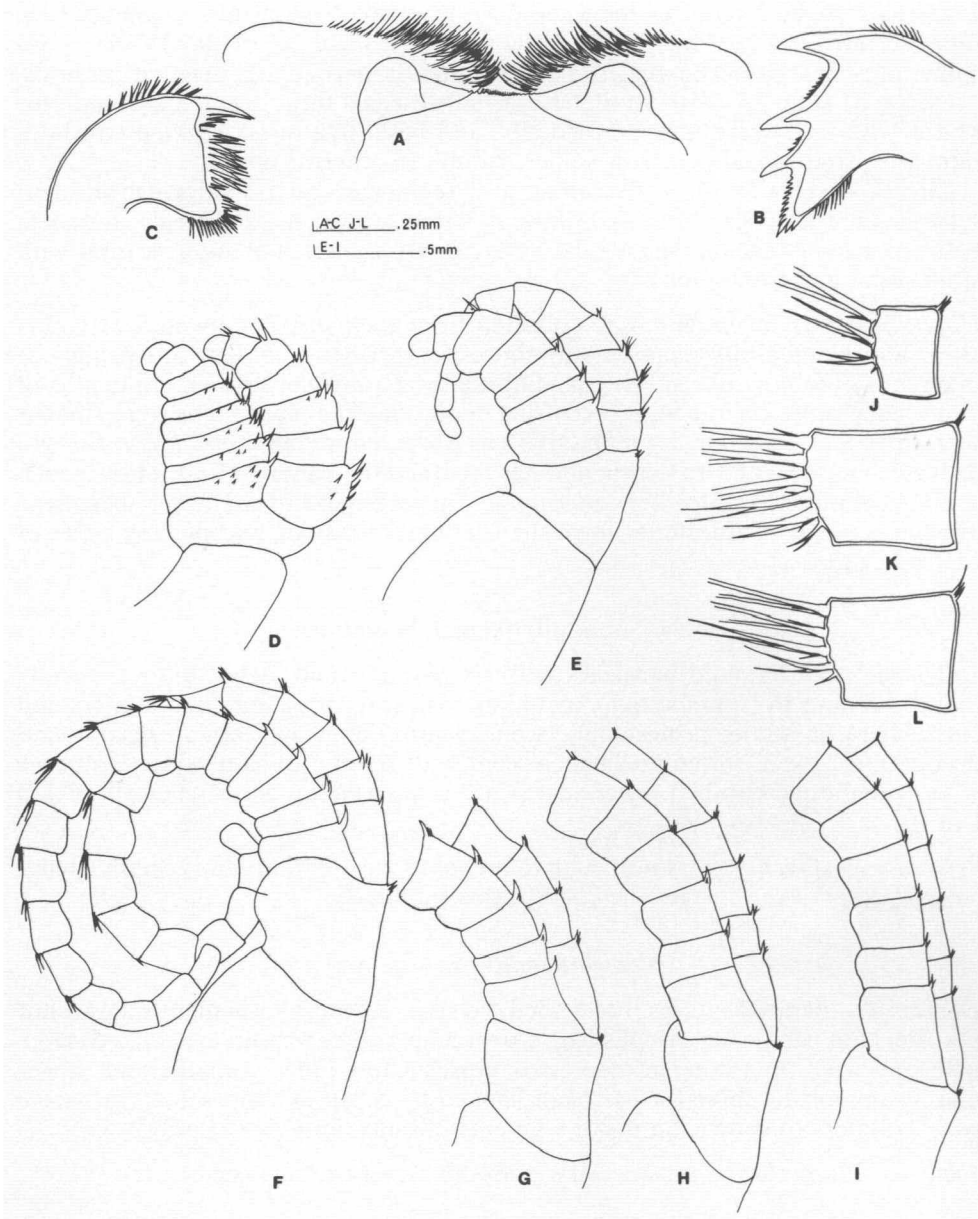


Figure 2. *Euraphia devaneyi* new sp., appendages of a 15-mm basal diameter specimen: A, labrum and mandibular palps; B, mandible; C, maxillule; D-F, cirri I-III with setae omitted but showing posterior distal spines; G-I, basal parts of cirri IV-VI; J-L, segments 22, 3 and 12 of the anterior ramus of cirrus VI.

Cirrus I (Fig. 2D) with short rami of wide segments, very setose medially with many finely serrate setae, with prominent spines on outer face of the anterior ramus, and especially prominent at distal angles at posterior edges of both rami.

Cirrus II (Fig. 2E) with the anterior ramus short and like the posterior ramus

of cirrus I. Posterior ramus longer and narrower with basal five segments with finely serrate setae medially, more distal segments like those of cirri IV–VI. Stout spines present at posterior angles of basal segments, particularly in anterior ramus.

Cirrus III (Fig. 2F) with similar length rami, basal three segments of anterior ramus with finely serrate setae medially, and basal five or six segments of both rami with stout distal posterior spines, stouter in anterior ramus.

Cirri IV–VI (Fig. 2G–L) with similar rami, segments with 3–5 pairs of prominent setae on anterior edge (more than three in larger specimens) and single short seta between bases of each large pair. Basal five or six segments of anterior rami with stout distal posterior spines.

*Habitat.*—Large specimens were collected from rock surfaces covered with coralline and filamentous algae on surf shores, occurring as solitary individuals or in clumps of four or five specimens. Subtidally, *E. devaneyi* extends to depths of 10 m being more cryptic with increasing depth. Subtidal specimens were smaller than intertidal ones. Dr. Luis DiSalvo has observed a crab, *Carpilius convexus*, eating *E. devaneyi* at 3-m depth, and has recorded the barnacle from the stomach contents of pufferfish, *Arothron meleagris*. The larger size of shallower specimens may reflect relative immunity from the small-sized rasping and picking fishes of Easter Island.

#### New Subfamily Notochthamalinae

*Diagnosis.*—Chthamalid barnacles with six parietal shell plates, ontogenetically reduced to four in *Chamaesipho*, including rostrum, carina and paired latera and rostrilatera, in some species concrescent. Scutum elongate; tergum narrow and deeply interlocked, sometimes concrescent with scutum of same side. Mandible with or without a combed lower edge. Card setae develop on some or all of cirri I to III.

*Etymology.*—GK *notos* = south, with reference to the predominantly South Pacific biogeography of the species included in this subfamily.

#### *Notochthamalus* new genus

*Diagnosis.*—Parietal sutures interfolded, no concrescence; basis membranous but may develop narrow calcareous ledge; opercular valves remain articulated, terga with one wide pit for tergel depressor muscle; mandibles pentadentoid, lower margin supporting three further teeth flanked by comb of short setae; card setae with 2–3 pairs of spines, on distal segments of both rami cirri II only.

*Type.*—*Chthamalus scabrosus* Darwin, South America. One species.

#### *Nesochthamalus* new genus

*Diagnosis.*—Parietal sutures interfolded, become concrescent by secondary calcification which also forms inflected calcareous basal margin; basis membranous; opercular valves become concrescent on each side; mandibles tridentoid (marginal spines between 1, 2 and 3), lower margin pectinate with 4–6 stout spines; card setae, when present, with four pairs of spines on distal segments of anterior ramus cirri II and proximal segments of anterior ramus cirri III.

*Type.*—*Chthamalus intertextus* Darwin, Philippine Archipelago. 1 species. Neso = island, with reference to its Pacific Island distribution.

*Rehderella* new genus

**Diagnosis.**—Parietal sutures interfolded, no concrescence; basis membranous; opercular valves become concrescent on each side, tergum with free crests for tergal depressor muscle; mandibles tridentoid (marginal spines either side of 3), lower margin with comb of short setae; card setae with 3–4 pairs of spines on distal segments of both rami of cirri II and proximal segments of anterior ramus and basiopodite of cirri III; caudal appendages present.

**Type.**—*Chthamalus belyaevi* Zevina and Kurshakova, Easter Island. One species. Named in honor of Dr. H. A. Rehder. Because the original description of *R. belyaevi* is limited, a supplementary description is given here.

*Rehderella belyaevi* (Zevina and Kurshakova)

Figures 1F–J, 3

**Synonymy.**—*Chthamalus belyaevi* Zevina and Kurshakova, 1973: 187; Newman and Ross, 1976: 41.

**Material Examined.**—Easter Island—Paratype, 8 May 1958 (G. Zevina, leg.); numerous specimens, intertidal, Hanga Roa, Vinapu, Vaihu, Anakena, 20–23 November 1976 (BAF coll., included 1st and 3rd topotypes); 10 specimens intertidal, 8 February 1983 (L. H. DiSalvo coll.). Pitcairn Island—12 specimens, intertidal, Christian's Point, 31 January 1972, with two specimens of *N. intertextus* (WAN and the late L. E. Ritchie coll., included 2nd topotype); 12 specimens, intertidal, St. Paul's Pool, 28 March 1982 among *N. intertextus* (J. Holdway coll.).

**Deposition of Types.**—(1) 1st topotype, U.S.N.M. Cat. No. 233268 (dissected); (2) 2nd topotype, U.S.N.M. Cat. No. 233269 (dissected); (3) 3rd topotype lot, Brit. Mus. (Nat. Hist.) Reg. No. 1987-3 (in alcohol, undissected).

**Distribution.**—Easter Island, Pitcairn Island (Fig. 4).

**Supplementary Description.**—Shell depressed. When young and uneroded (Fig. 1F), translucent with wide alae on carina and rostrum, parietes folded longitudinally. In older specimens (Fig. 1G, H), parietal sutures interfolded, sometimes obliterated in extremely corroded shells. Shell internally smooth, without inflected basal margin. Basis membranous.

Tergum and scutum (Fig. 1I) on each side calcified together in all but very youngest specimens; internally with faint scar for scutal adductor muscle, 6–8 depending crests for tergal depressor muscle, position of tergal scutal junction indicated by slight step in basal margin.

Labrum wide, shallowly concave with row of blunt teeth. Mandible (Fig. 3A, B) with three teeth, denticulate on upper edges of third and second in larger specimens, and with short row of setae on lower angle. Maxillule (Fig. 3C) with three prominent spines at upper angle, and few longer spines placed centrally between others along cutting edge.

Cirri I and II (Fig. 3D, E) short, with subequal rami of 4–7 segments, with card setae (Fig. 3K) with 3–5 side teeth on each side on distal segments of cirrus II. Cirrus III (Fig. 3F) slightly shorter than posterior cirri, segments similar to those of posterior cirri except for basal four or five of the anterior ramus and the basiopodite which are thicker, setose medially and carry card setae like those distally on cirrus II. Cirri IV–VI (Fig. 3H, J) with up to 15 and 17 segments in cirri IV and VI respectively; segments with 4–6 pairs of setae on anterior edge, with small seta between the base of the upper 4 pairs.

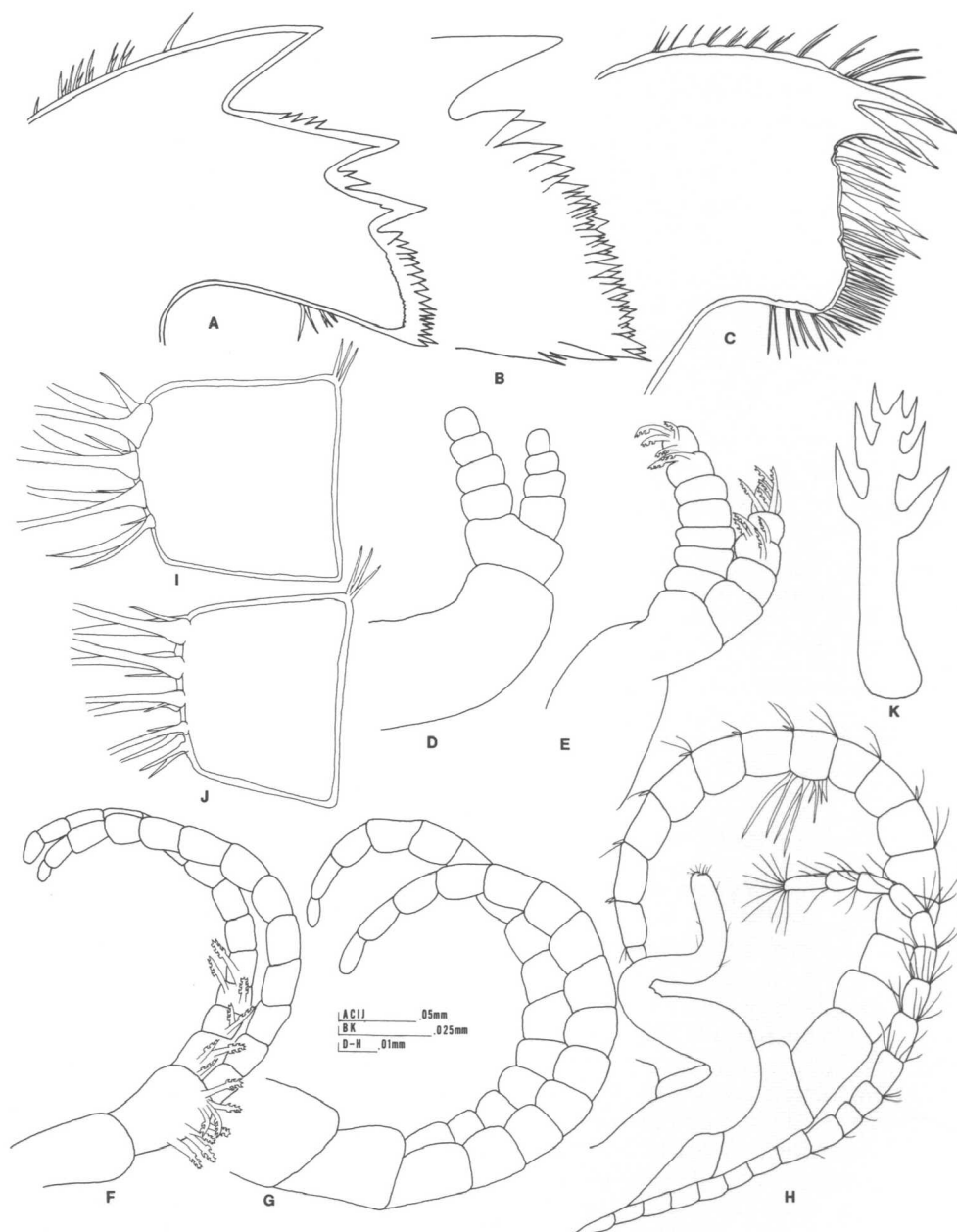


Figure 3. *Rehderella belyaevi* new genus, appendages of a 7-mm diameter specimen from Easter Island: A, B, mandible; C, maxillule; D-G, cirri I-IV; H, cirrus VI and caudal appendages; I, J, segments 8 and 12 of cirrus VI; K, card seta from cirrus II or III.

Specimens less than 5-mm diameter do not possess cards, and in larger specimens their distribution is variable. The maximum number per segment observed was five on a distal segment of cirrus IIa on one side but frequently there is only one per segment. The maximum number of segments seen to carry cards in any one ramus was the apical five segments in cirrus IIa, three in cirrus IIp, and the

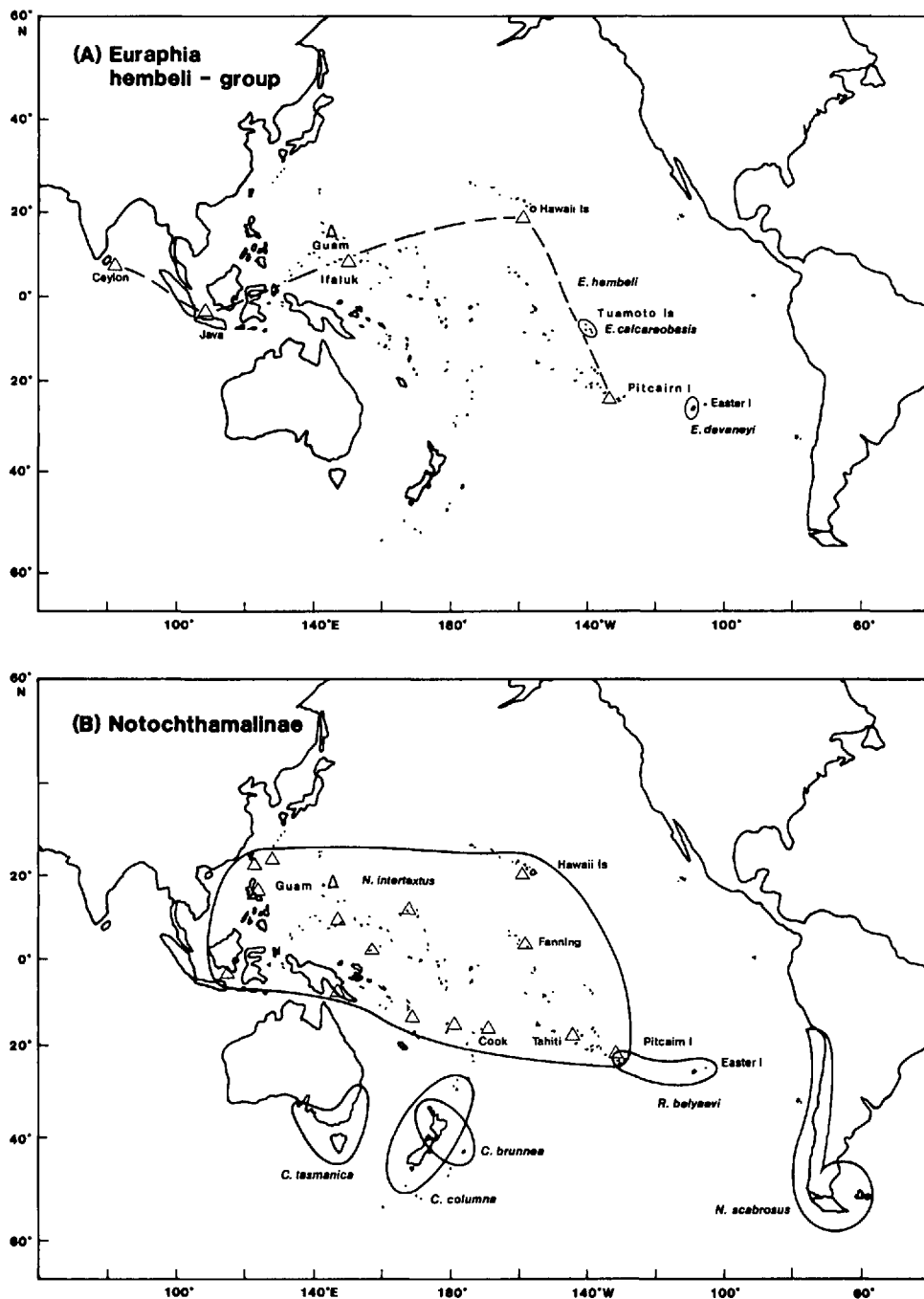


Figure 4. A: Distribution of *Euraphia hembeli*-group. After Nilsson-Cantell, 1921; Henry, 1957; Newman and Ross, 1976; new records for *E. hembeli* Pitcairn (J. E. Randall and D. Devaney coll., 31 December 1970, 0–1.3 m, Bernice P. Bishop Museum acc. no. 71.201), Ceylon (Beruwala, W. D. Hartman and A. J. Kohn coll., 1961, Yale Peabody Museum no. 4349), Guam (BAF coll., 27 June 1986); *E. devaneyi*, this paper. B: Distribution of Notochthamalinae. *N. scabrosus* after Newman and Ross (1976); *Chamaesipho* spp. after Foster and Anderson (1986); *N. intertextus* after Newman and Ross (1976) plus new records from Fanning Island (WAN), Cook Islands (A. S. W. Penniket coll., 30 October 1978), Tahiti (BAF coll., November 1976), Pitcairn Island (WAN and L. Ritchie, see under *R. belyaevi* this paper), Guam (BAF coll., 27 June 1986); *R. belyaevi* this paper.



basal three in cirrus IIIa. No specimens of *R. belyaevi* greater than 5-mm basal diameter, were found without cards.

Caudal appendages (Fig. 3H) initially a pair of protuberances with distal setae in small specimens (less than 4-mm diameter and in which penis also short), but with up to 20 segments in large specimens and as long as cirrus VI.

*Maximum Size.*—9-mm rostracarinal diameter, 2-mm high.

*Habitat.*—On Easter Island, *R. belyaevi* forms closely packed sheets on the upper intertidal rocks which experience surf wash. During calm seas, these barnacles are fully sun-exposed. It co-occurs with two grazing snails, *Nodolittorina pyramidalis pascuensis* and *Nerita morio*, but otherwise occurs above and apart from the encrusting and filamentous algae and other obvious macrofauna on the shores. The lower limit is at least partly set by predation by the whelk *Neothais nesiotes* (Kohn, 1978). Small individuals of *R. belyaevi* with persistent, brown cuticle are found in crevice habitats, in association with *Tesseropora* sp. and *E. devaneyi*, and also amongst adults, but large barnacles are restricted to open rock surfaces.

#### *Chamaesipho* Darwin

*Diagnosis.*—Parietal sutures not interfolded, become concrescent firstly by fusion of latera and rostrilatera, then all; basis membranous; opercular valves remain articulated, terga with pits; mandibles tri- or quadridentoid, lower margin with comb of short setae with or without included short teeth; card setae with 2–5 pairs of spines, on distal segments of posterior ramus cirri I (*C. brunnea* only), distal segments of anterior ramus of cirri II, and proximal segments of anterior ramus and basipodite of cirri III.

*Type.*—*Chamaesipho columna* (Spengler) sensu Darwin, New Zealand (Foster and Anderson, 1986).

*Remarks.*—The genus now contains three species. *C. columna* and *C. brunnea* from New Zealand, and *C. tasmanica* from Australia (Foster and Anderson, 1986). Darwin's *C. scutelliformis* Darwin has been assigned to monospecific genus, *Chinochthamalus* (Foster, 1982).

#### DISCUSSION

*Relationships within the hembeli-group of Euraphia.*—*E. devaneyi* most closely resembles *E. hembeli* Conrad known from a few Indo-West Pacific localities from Ceylon to Hawaii and Pitcairn (Fig. 4). *E. hembeli* is notable for its large size, for a chthamalid. Pilsbry (1916) gives maximum dimensions of 49-mm shell height and 76-mm basal diameter. Such large shells, as figured by Darwin (1854) and Pilsbry (1916), are often externally much eroded. So too are the larger specimens of *E. devaneyi* from Easter Island. As many characters are modified during ontogeny and by environment, care has been taken in making comparisons.

In comparable sized and uneroded barnacles, *E. devaneyi* is distinguished from *E. hembeli* by the external longitudinal ridging of the parietes, and by the lack of longitudinal impressed grooves and the narrowness of the scutum.

The internal body parts of *E. hembeli* are described by Nilsson-Cantell (1921) and Henry (1957). In *E. devaneyi*, the maxillule has a deeper notch below the upper group of spines, the segments of the posterior cirri lack tufts of small spines between the bases of the major setae on the anterior edge, and the distal posterior angles of the basal segments of the cirri bear one or two strong spines, more prominent than those in *E. hembeli*.

A third species, *E. calcareobasis* Henry from the Tuamotu Islands, is also closely related. Some of the differences between *E. hembeli* and *E. calcareobasis* enumerated by Henry (1957) have been amended by Newman (1961), in particular the supposed differences in the base. Whereas all three species develop calcareous bases, older specimens of *E. hembeli* and *E. devaneyi* internally overlay the basis and paries with secondary internal secretion of shell.

*E. calcareobasis* has some similarities with *E. devaneyi* that are not shared with *E. hembeli*, in particular the general shape of the opercula, the notched maxillule, and the absence of short bunches of spines between the major setae on the posterior cirri. *E. calcareobasis* too has been collected subtidally on coral (*Millepora*) and in this respect it and *E. devaneyi* differ from other chthamalids.

The subtidal occurrence is unusual for chthamalid barnacles. The lower shore to subtidal barnacles are preyed on by at least crabs and pufferfish. Other fish also contained shells of *Tesseropora* sp. in their stomachs (from specimens and information supplied by Dr. DiSalvo), so predator influence is clearly operating on Easter Island barnacle populations. It is tantalizing to suggest, however, that reduced predator and/or competitor pressures associated with biotic impoverishment of eastern Polynesian ecosystems may permit wider niche occupancy.

Of these three closely-related species, *E. calcareobasis* and *E. devaneyi* are peripheral insular endemics of southeastern Polynesia. *E. hembeli*, on the other hand, while also known from southeastern Polynesia (Pitcairn) is more widely distributed in the Indo-West Pacific Ocean. The uncombed, incisiform mandible of *Euraphia* is also a feature of *Catophragmus imbricatus*, *Catomerus polymerus*, *Octomeris angulosa* and *O. brunnea*, and in view of obvious shell pleisomorphies of these balanomorphs the incisiform, tridentoid mandible is considered also to be pleisomorphic.

*Unity of the Notochthamalinae.*—*R. belyaevi* has three special features: caudal appendages, the concrescent tergum and scutum on each side, and the card setae on cirri II and III. Taking these in turn, caudal appendages are a common feature of lepadomorph barnacles and are regarded as a pleisomorphic character and therefore not indicative of a close relationship between *R. belyaevi* and the only other six-plated chthamalid to possess them, *E. caudata*. Concrescence of the opercula of the adult is more likely an apomorphy indicating relationship. It could be argued that it is a convergent development in *R. belyaevi* and *N. intertextus* since they occupy similar habitats, and in fact co-occur on Pitcairn Island. However, a close relationship between these two tropical species is indicated by their possessing card setae on cirri II and III.

A past difficulty in recognizing the relationship between *N. intertextus* and *R. belyaevi* has been the non-combed lower margin of the mandible of the former and the combed mandible of the latter (Fig. 5). The mandible of *R. belyaevi*, like that of *N. intertextus* and *C. brunnea*, is basically tridentoid, albeit with spinose superior margins to the second and third teeth. A similarly tridentoid mandible occurs in *Catomerus polymerus*, and a quadridentoid mandible (supposed characteristic of Chthamalinae by Newman and Ross, 1976) with side cusped teeth occurs in *Octomeris angulosa* (included in the Euraphiinae by Newman and Ross, 1976). The number of teeth on the mandible is, therefore, judged not to be as definitive a character as formerly supposed. Certainly, the incisiform tridentoid mandible is a pleisomorphy like the caudal appendages, but a combed lower margin and the development of extra teeth are probable apomorphies, resulting in more molariform mandibles amongst the Notochthamalinae and Chthamalinae.

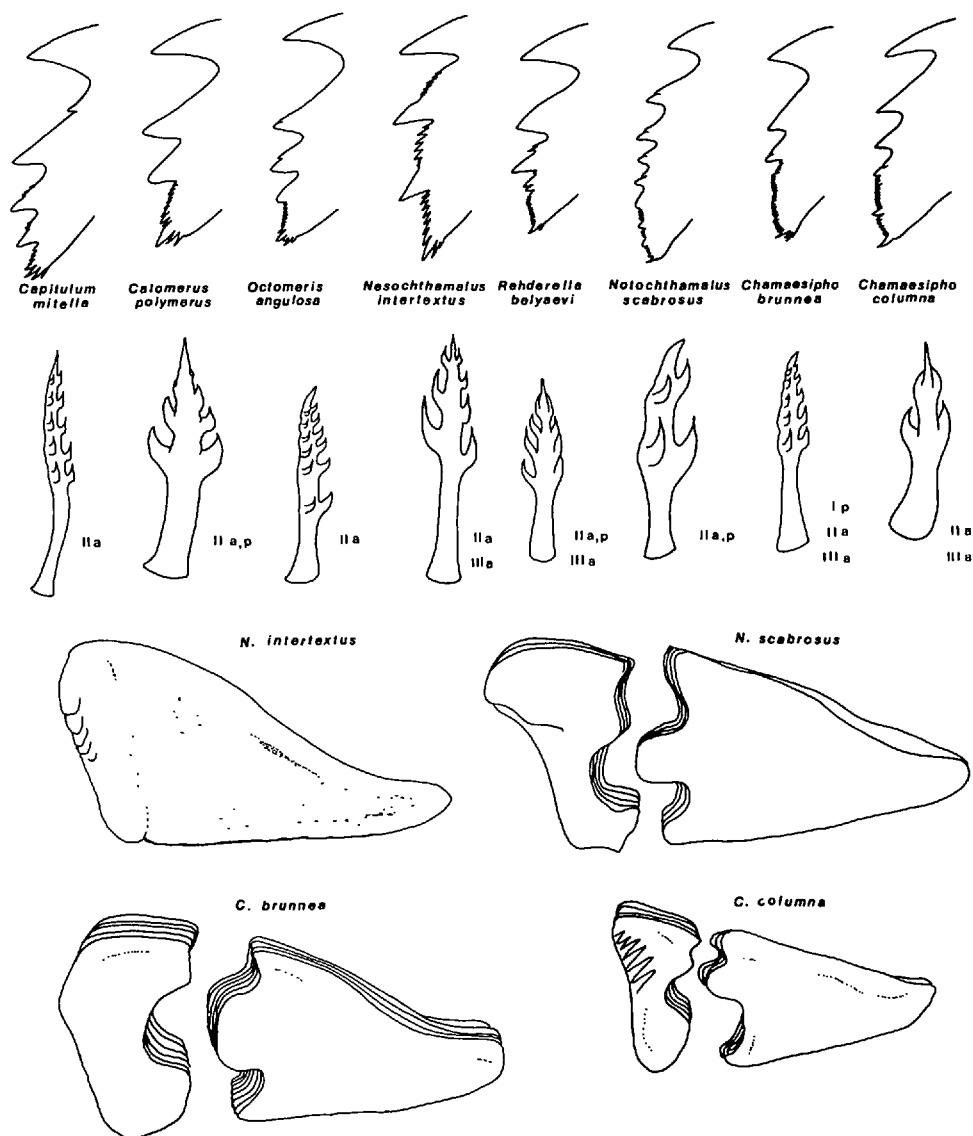


Figure 5. Comparison of mandibles (top), card setae (middle) and opercula (bottom) of Notochthamalinae and other intertidal barnacles. Card setae, drawn here from scanning electron micrographs, may occur on the anterior (a) or posterior (p) rami of cirri I–III as indicated. Size and locality for individuals providing opercula: *N. intertextus* 8.5 mm, Fiji; *N. scabrosus* 8.2 mm, Punta El Lacho, Chile; *C. brunnea* 11.8 mm, New Zealand; *C. columna* 5.5 mm, New Zealand. See Figure 1 for fused opercula of *R. belyaevi*.

Specialized setae of the anterior cirri are known for a wide range of barnacles, mostly from intertidal balanomorph species and also in the intertidal scalpellid *Capitulum mitella* (cirrus II only), and in *Pollicipes polymerus*, *Calantica spinosa* and *C. villosa* (cirri II and III)—(Pope, 1965; Newman and Ross, 1976; Foster, 1978; Dando and Southward, 1980; and new observations). Notochthamaline setae termed cards in this paper are the “grapple setae” of Pope (1965). They are antler-like, and stouter than most specialized setae, except for those of *Capitulum*

*mitella*, *Catomerus polymerus* and *Octomeris angulosa* (Fig. 5). In these last three species the cards are restricted to the distal segments of cirrus II. This too is the situation in *N. scabrosus*, but in other species herein assigned to the Notochthamalinae the cards also occur proximally in cirrus III and even apically in cirrus I of *C. brunnea*.

The variability of occurrence and distribution of cards in *R. belyaevi* is commented on above. In *N. intertextus*, their occurrence is even more variable, with many large specimens devoid of them. None were seen in specimens from the Caroline, Marshall, Line and Hawaiian Islands. They were absent in 2 out of 9 specimens from Fiji, and 15 out of 22 from Rarotonga, but present in all of the few specimens available from Tahiti and Pitcairn Island. In specimens that had them, the maximum number per segment observed was five, on any, rarely all, of the apical five segments of ramus IIa (frequently absent from the distal segment) and the three basal segments of ramus IIIa (never on the basiopodite). The maximum number of cards for any one specimen was eight.

The variability of the distribution of cards is also a feature of *N. scabrosus* in which they are restricted to cirrus II. Apart from this observed variability, there are presently no particular reasons for suspecting significant genetic differences between populations of *N. intertextus* in various parts of the western Pacific, or of *N. scabrosus* in its long range from Peru to the Falkland Islands, but notice is taken of recent studies of Atlantic chthamalid barnacles (Southward, 1975; 1976; 1983; Dando and Southward, 1980; 1981; Crisp et al., 1981) which have revealed the existence of long confused sympatric species which externally look alike, particularly in the eroded state.

The operculum of *N. scabrosus* closely resembles that of *Chamaesipho* spp. from the opposite side of the South Pacific Ocean (Figs. 4, 5). *Chamaesipho* also has card setae on anterior cirri, and consistently so (Foster and Anderson, 1986). *Chamaesipho tasmanica* from Australia morphologically resembles *C. columna* from New Zealand more than *C. brunnea* which is also from New Zealand. Foster and Anderson (1986) suspect that *C. columna* is an evolutionary development which has involved faster growth rates to maturity, and possible special feeding and sensory abilities associated with antenniform anterior cirri which neither *C. tasmanica* nor *C. brunnea* possess.

**Biogeography of Easter Island Barnacles.**—The marine fauna of Easter Island shows considerable species poverty and disharmony as expected with such oceanic isolation (Gressitt and Yoshito, 1963). Only 112 species of shallow water molluscs (Rehder, 1980), 99 species of fish (Randall, 1976; Springer, 1982), 7 species of echinoids (Fell, 1974), 6 species of scleractinian corals (Wells, 1972), 7 species of natant decapods (Holthuis, 1972) and 3 pagurid decapods (Dr. P. McLaughlin, pers. comm.) are known. The barnacles are no exception. The marine fauna of the Rapanuian Province (Easter Island and Sala Y Gomez, with Rapa, Pitcairn, Oeno, Ducie) is generally held to have clear Indo-West Pacific affinities, but one of the barnacles, *R. belyaevi*, also has southern ocean relatives in the subfamily Notochthamalinae.

Interestingly among the wider family Chthamalidae, the more pleisomorphic species are southerly ones, endemics in isolation on southern outposts. The Notochthamalinae, except for *N. intertextus*, seem to represent good cases of Pacific Basin peripheral relics, conforming to Théel's (1886) and Rehder's (1980) concepts of "competitive displacement" of older faunas to the fringes of their original range, which when linked to a tropical center of origin leads to peripheral survival of primitive species at higher latitudes. The two chthamalid barnacles of Easter

Island are apparently further examples of Pacific Basin peripheral endemism, not at midlatitudes but furthest southeast. Marked endemism of the insular Rapanuian or Hawaiian Provinces (Springer, 1982), raises questions about modes of arrival of the species or their ancestors, and the shortness of geological time available for their accumulation on such young islands where the probability of extinction must be great. In the Tertiary context, elements of larval dispersal must be involved.

Many of the non-endemic molluscs documented by Rehder (1980) that are rare in Easter Island but widespread in the west Pacific give the impression of waifs. Dispersal of larvae or other propagules from, say, the Tuamotu or Austral Islands may occur, especially if we invoke the aid of meteorological anomalies such as hurricanes that speed up and alter surface currents to provide occasional rare and rather accidental opportunities (Gulick, 1932). However, the general westerly flowing surface currents in the region seem opposed to regular dispersion from the west. Hydrological accounts of the region show Easter Island situated near the center of the great subtropical gyre of the eastern South Pacific Ocean (Wyrki, 1966). It is a region of weak currents (U.S. Naval Oceanographic map SP-68), and of low zooplankton densities (Fisher, 1958). Larval dispersal to Easter Island must cover minimum sea distances of 2,200 km from the west (Pitcairn) and 2,860 km from the east (San Felix and San Ambrosio). There is no evidence that shore species without teleplanic larvae have this ability, and plausible explanations have to invoke ancient archipelagos with short inter-island distances (Newman and Foster, 1983).

The endemism of *E. devaneyi*, distinct from *E. calcareobasis* of the Tuamotus and *E. hembeli* with a wide but apparently patchy and insular distribution in the Indo Pacific, points to effective isolation of past stock. Its speciation requires that there has been sufficient time, and for Easter Island 2.5 million years are available (Heirtzler et al., 1968). There is no way of knowing whether this is long enough, but it is conceivably so. It is with respect to *R. belyaevi* that the island age seems insufficient. The lineage of this barnacle with pleisomorphic caudal appendages must have involved a stock older than either Pitcairn or Easter Island. A solution has been sought in hypothesizing tectonic creation of islands near the East Pacific Rise at these latitudes for the last 30 million years (Springer, 1982; Newman and Foster, 1983). As erosion and subsidence drowned these islands, and as they moved apart to either side of the Rise by sea-floor spreading, the shore species dispersed to nearby, newly-formed islands.

Where the stock of *R. belyaevi* came from in the first place is an open question. The notoichthamalines could represent fragments of ancient southern ocean shore faunas which became isolated from each other during past tectonic events. Affinities with *N. scabrosus* of South America tempt an east-to-west "tract" across the Pacific involving ancient Nasca Ridge archipelagos. There is otherwise limited marine faunal relationship with South America. The occurrence of the macruran *Rhynchocinetes balsii* from Easter, Juan Fernandez and New Zealand (Holthuis, 1972) may involve teleplanic larvae and different geographical relationships.

*R. belyaevi* might also be regarded as an ancient immigrant to the Easter Island region from the west where it is now replaced by the more advanced *N. intertextus*. *R. belyaevi* could be viewed as a species surviving as a refugee in furthest Oceania, where it may or may not have changed in its long island-hopping isolation. Rehder (1980) favored such a model of species displacement to account for molluscan peripheral endemism in Polynesia, and despite the likely involvement of moving plates and islands, inter-island dispersal must have been involved.

Whatever the earliest origins, the population of *R. belyaevi* is now split into at

least two populations, on Pitcairn and Easter Islands, which are moving apart as the sea floor spreads away from the East Pacific Rise west of Easter Island. The two populations could be genetically isolated, but available material and conventional morphological criteria fail to sustain this. Survival of either population will depend on the tectonic creation of new islands in the region before the existing ones are eroded and translated below sea level.

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